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BCM Network develops Orientation Selectivity and Ocular Dominance in Natural Scene Environment.

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Abstract

A two-eye visual environment is used in training a network of BCM neurons. We study the effect of misalignment, between the synaptic density functions connecting both eyes to each single neuron, on the formation of orientation selectivity and ocular dominance. The visual environment we use is composed of natural images. We show that for the BCM rule a natural image environment with binocular cortical misalignment is sufficient for producing networks with orientation selective cells and ocular dominance columns. This work is an extension of our previous single cell model (Shouval et al., 1996).

1 Introduction

It is generally accepted that both orientation selectivity and ocular dominance of receptive fields in the visual cortex of cats are dramatically influenced by the visual environment (for a comprehensive review see, Frégnac and Imbert, 1984). Organization of the different properties of receptive fields such as ocular dominance and orientation selectivity across the visual cortex is best observed by optical imaging techniques (Bonhoeffer and Grinvald, 1991; Blasdel, 1992). To the best of our knowledge, these methods have not been used yet to examine how receptive field organization is influenced by changes in the visual environment. It has been shown that the anatomical correlates of ocular dominance columns, can be altered by changes to the visual environment (Hubel et al., 1977, eg). Furthermore the assumed model of plasticity, will influence the structure of receptive field organization in the mature cortex (Erwin et al., 1995).

Different models attempting to explain how cortical receptive fields evolve have been proposed over the years (von der Malsburg, 1973; Nass and Cooper, 1975; Perez et al., 1975; Sejnowski, 1977; Beienenstock et al., 1982; Linsker, 1986; Miller, 1994). Such models are composed of several components: the exact nature of the learning rule, the representation of the visual environment, and the architecture of the network. Most of these models assume a simplified representation of the visual environment (e.g. von der Malsburg, 1973), or replace the visual environment by a second order correlation function (Miller, 1994).

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Realistic representations of the visual environment have only very recently been considered (Hancock et al., 1992; Law and Cooper, 1994; Shouval et al., 1996; Olshausen and Field, 1996b), and only in recent years have the statistics of natural images been studied and used for predicting receptive field properties (Field, 1987; Field, 1989; Atick and Redlich, 1992; Bialek et al., 1991; Liu and Shouval, 1994; Shouval and Liu, 1996). Once actual visual scenes are used, it is possible to realistically represent two-eye input, and account for the fact that the two eyes are not looking at exactly the same visual scene. For example, Li and Atick (1994) have used natural images to extract detailed two-eye power spectra from stereo images. They have used these results to predict properties of cortical receptive fields.

We have recently shown(Shouval et al., 1996) that single cell BCM neurons, trained in a binocular natural image environment can develop both orientation selectivity and varying degrees of ocular dominance. We have also shown in that study that PCA(Oja, 1982) neurons can not develop ocular dominance as a result of the invariance of the two-eye correlation function to a two-eye parity transformation.

In this paper we extend this study to networks of interconnected neurons. The network interactions have two types of affects:

(a) They can alter properties of single cell receptive fields.

(b) They produce an organization of receptive fields across the cortex.

We examine here these two types of effects.

Unlike our previous study, we do not present results using the PCA rule since in that case the network does not qualitatively affect the single neuron results and in particular all cells remain binocular. This result can be shown to follow from an extension of the two-eye parity method to linear networks.

Recently several models that attempt to generate sparse coding have been proposed for learning in early visual cortex (Földiák, 1990; Fyfe and Baddeley, 1995; Olshausen and Field, 1996b). In this paper we demonstrate that BCM neurons achieve sparse coding (Intrator and Cooper, 1992) without explicitly attempting to maximize the spareness.

2   Details of the model

The BCM theory (Beienenstock et al., 1982) was introduced to account for the striking dependence of the sharpness of orientation selectivity on the visual environment. We have used a variation, due to Intrator and Cooper (1992), for a nonlinear neuron with a non-symmetric sigmoidal transfer function. Using the above notation, synaptic modification is given by:

$$\dot{m}_j(\mathbf{x}) = \eta \phi(c(\mathbf{x}), \Theta_M(\mathbf{x})) d_j, \tag{1}$$

where the neuronal activity is given by c, $\phi(c(\mathbf{x}), \Theta_M(\mathbf{x})) = c(\mathbf{x})(c(\mathbf{x}) - \Theta_M(\mathbf{x}))$, $\mathbf{x}$ denotes the coordinates of the neuron within the network, m_j are the synaptic weights, d_j the inputs and Θ_M is the modification threshold. The modification threshold, Θ_M, is a nonlinear function of some time averaged measure of cell activity, given by

$$\Theta_M(\mathbf{x}) = E[c^2(\mathbf{x})], \tag{2}$$

where E denotes the expectation over the visual environment.
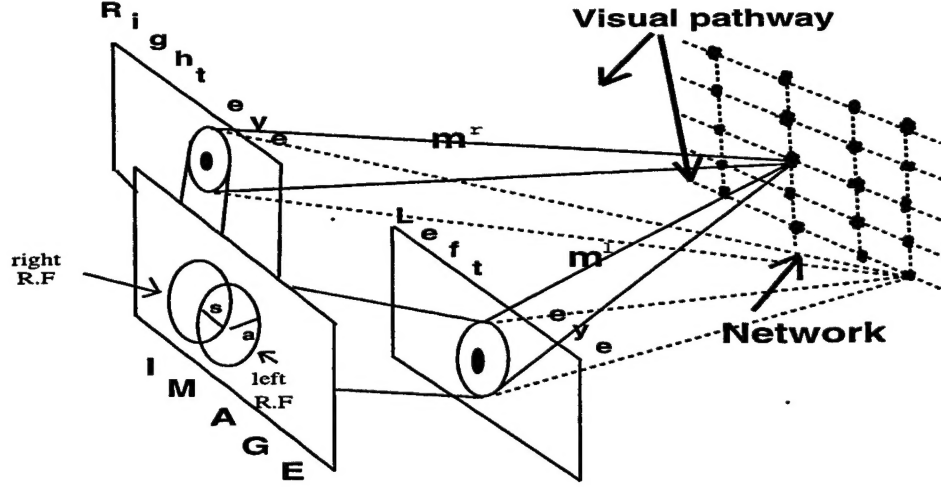
Binocular Model

Figure 1: Schematic diagram of the two eye model, including the visual input preprocessing. Different cells in this network receive the same partially overlapping inputs.

In the lateral inhibition network c is also a function of the activity of it's neighbors. The activity is given by[1]

$$c(x) = \sigma \left(\sum_{x'} I(\mathbf{x} - \mathbf{x'}) \sigma(\mathbf{m}(x') \cdot \mathbf{d}) \right) \tag{3}$$

Where I is the lateral interaction matrix for which we used a balanced DOG and is given by

$$I(\mathbf{x}) = (1/2\pi\sigma_E^2) \exp\left(-\frac{1}{2} \left(\frac{x}{\sigma_E}\right)^2\right) - (1/2\pi\sigma_I^2) \exp\left(-\frac{1}{2} \left(\frac{x}{\sigma_I}\right)^2\right)$$

Where σ_E and σ_I are the length scales of the excitation and inhibition respectively. The transfer function σ is non symmetric around 0 to account for the fact that cortical neurons show a low spontaneous activity, and can thus fire at a much higher rate relative to the spontaneous rate, but can go only slightly below it[2].

We have used the same visual environment that we have described in detail in our single cell study (Shouval et al., 1996). It is composed of a set of 24 natural images scanned at a $256 \, X \, 256$ pixel resolution. We have avoided man-made objects, because they have many sharp edges, and straight lines, which make it easier to achieve oriented receptive fields. We have modeled the effect of the center surround retinal and LGN projections, by convolving the images with a difference of Gaussians (DOG) filter, with a center radius of one pixel ($\sigma_1 = 1.0$) and a surround radius of three ($\sigma_2 = 3$) As illustrated in Figure 1, the input vectors from both eyes are chosen as small,

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[1] We have also used the type of lateral network described in Intrator and Cooper (1992) with the same I and found no qualitative difference in the results.

[2] The actual sigma used in the simulations is $(e^x - e^{-x})/(0.05e^x + 5e^{-x})$.

partially overlapping, circular regions of the preprocessed natural images; these converge on the same cortical cell.
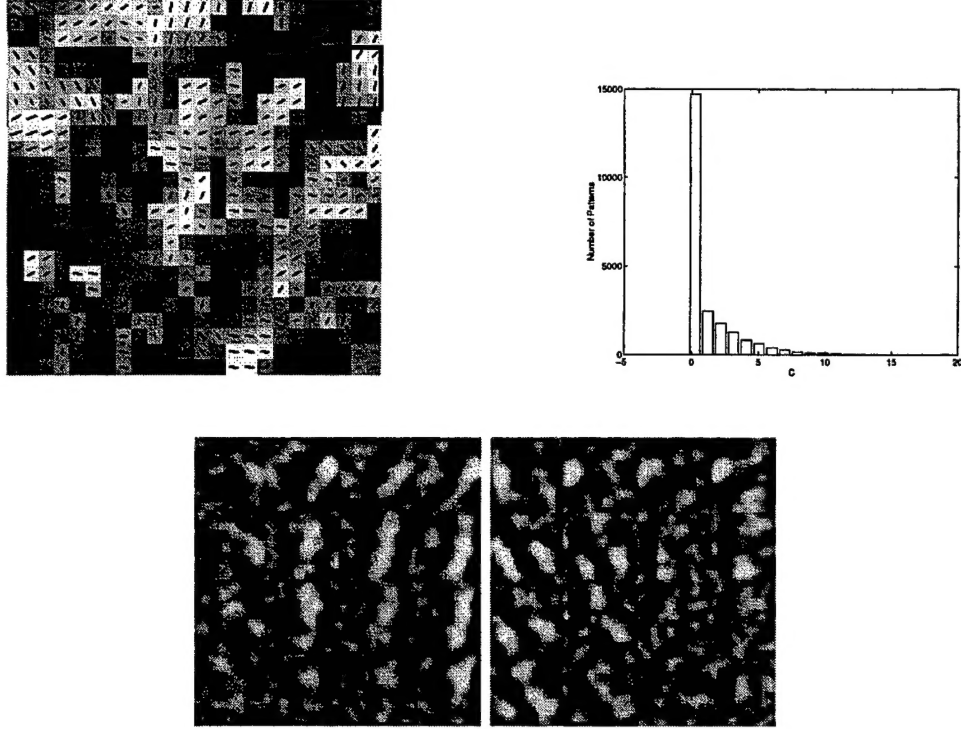
3 Results

Figure 2: The top left figure represents combined Ocular Dominance and Orientation maps extracted by a network of 24 by 24 neurons with receptive fields of diameter 20 and a shift of 15 pixels between the two eyes. For this network $\sigma_E = 1$ and $\sigma_I = 5$. The orientation of the bars codes for the preferred orientation of the cells, it's length represents the degree of orientation selectivity, the gray scale of the background represents Ocular Dominance. On the right is a histogram of the activity of all neurons in the network in response to 40 patterns chosen from the data set. We can see that the response is sparse; most neurons have a large response only a small fraction of the time. On the bottom the feed forward receptive fields from the 4 by 4 region of the network that is enclosed in the black box, are displayed. On the bottom right the connections to the right eye (m^r) and on the bottom left the connections to the left eye (m^l).

Figure 3 depicts results of a typical network. The receptive fields displayed in such networks are very similar to those obtained for single cells (Shouval et al., 1996; Law and Cooper, 1994). They are orientation selective to all orientations and show various degrees of ocular dominance. The degree of ocular dominance depends on the overlap between the receptive fields of the two eyes, larger overlaps producing more binocular cells.

The activity histogram displayed in the upper right hand side of figure 3 shows that the activity of neurons in the network is sparse.

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The organization of such receptive fields across the cortex, that is the organization of Ocular Dominance bands, Iso-Orientation bands and the relationship between them depends crucially on the details of the lateral interaction I, as can be seen in figure 3. It is possible to change the parameters of the lateral interaction in order to achieve cortical maps which exhibit a greater or a smaller resemblance to experimental cortical maps. However we do not attempt to explore that here, since we believe that cortical maps are influenced by many other factors such as innate preferences, the more complex three dimensional anatomy of the cortex, and the details of the imaging techniques used to obtain the maps.
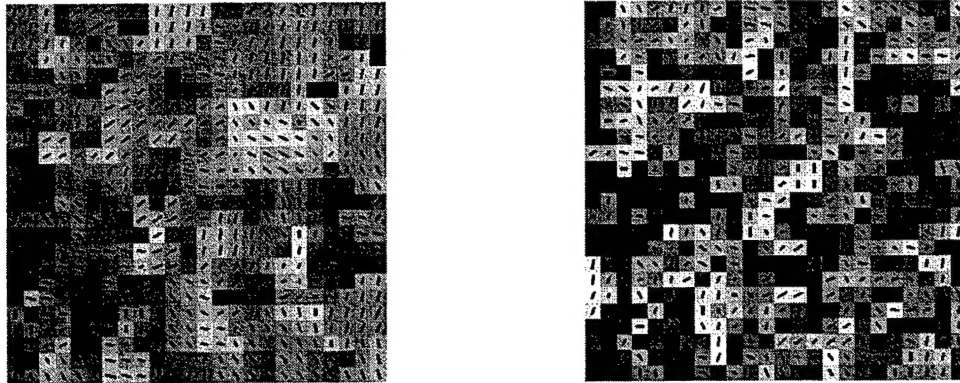

Figure 3: The effect of changing the parameters on network organization. On the left the effect of changing the overlap between the eyes is displayed. The displacement between the two eyes is 5 pixels, apart from that the parameters are identical to the one in figure 3. The Ocular Dominance bands become much weaker in this case. On the right the effect of changing the lateral interaction term I is displayed, here $\sigma_E = 0.7$ and $\sigma_I = 2$, apart from that the parameters are identical to the one in figure 3. This has the effect of greatly reducing the continuity in the orientation and Ocular Dominance.

4   Discussion

We have extended our single cell results (Shouval et al., 1996) to networks of connected neurons. The networks have been trained with a natural scene environment that was preprocessed with a DOG filter. The two eyes were exposed to small partially overlapping portions of these images. Like in our single cell study we have shown that orientation selective cells with varying degrees of ocular dominance develop. The degree of ocular dominance depends mostly on the overlap between the inputs.

Sparse neuronal representation can be roughly characterized by neuronal activity which is inactive most of the time, namely has a distribution of activity which is highly peaked at zero and thus has heavy tails. For this reason sparse activity is associated with kurtotic activity distribution. It is thus clear that various types of distributions, with the common property of having large peak at zero, will fit into this definition. The instantaneous sum of activity of a network of sparse neurons will have a Gaussian distribution if the neurons are independent (although each of them may be highly kurtotic) and will maintain its kurtoic shape if the code is also non redundant. In the case of n linearly independent clusters in an n dimensional space, it has been shown (Intrator and Cooper,

1992) that a network of n BCM neurons will find a solution so that the weight vector of each neuron is orthogonal to all but one of the cluster centers. In other words, if cluster i appears with probability p_i, the neuron that becomes selective to this cluster is inactive with probability $1 - p_i$. Furthermore, when it is active, the neuronal activity C_i is proportional to $1/p_i$. Thus the sum of n such neurons - C, has a distribution in which the tail decays as $1/C$ (Figure 3, right). This is certainly heavier than the tail of a Gaussian distribution which decays as $\exp(-C^2)$.

We emphasize that in the BCM network case, sparse coding is an outcome of the dynamics of the BCM learning and is not specifically built into the code generation process as is done in (Olshausen and Field, 1996a). Furthermore, in accordance with Barlows predictions (Barlow and Pettingrew, 1971), events that occur with high probability are conveyed by a less active neuron than events which occur less frequently. Such events will be conveyed by a neuron that is quiet most of the time, but fires strongly when the event is detected. It will be interesting to compare the resulting code with methods that maximize sparsity or kurtosis as a goal for neuronal coding and feature detection (Földiák, 1990; Fyfe and Baddeley, 1995; Olshausen and Field, 1996b).

The organization of receptive fields across the cortex, presented above, includes many of the components required from a cortical map. It has both ocular dominance columns and varying orientation preference. The orientation map has both linear regions and non-linear regions in which sharp transitions in orientation preference occur. The organization of receptive fields across the cortex depends critically on the parameters of the lateral interaction term, but we believe that in the real visual cortex, cortical maps are influenced as well by other factors such as innate preferences, the more complex three dimensional anatomy of the cortex and the shape of the boundaries of the cortical area.

As far as we know this is the first network model, trained in a natural image environment, which develops concurrently both ocular dominance and orientation selectivity. The model presented recently by Olshausen and Field (96) develops orientation selective neurons from a natural image environment, however it does not attempt to model the binocular aspects of cortical cells or the organization of these receptive fields across the cortical sheet.

5   Acknowledgments

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